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Mangrove Floristics and Biogeography

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4.1 Introduction

Mangroves are a diverse group of predominantly tropical trees and shrubs growing in the marine intertidal zone where conditions are usually harsh, restrictive and dynamic. Here, they are subject to both shorter term rhythms of tides and seasons, as well as longer term changes of climate and sea level. As a group, they share several highly specialized and collectively well-known adaptations, notably exposed breathing roots, support roots and buttresses, salt-excreting leaves, and viviparous water-dispersed propagules. However, as individuals, we know less about them, exemplified by the mistaken belief that these characters might be shared equally by all species. Therefore, in this chapter, it was necessary first to clarify and enhance the concept and definition of what is a mangrove, prior to discussing their biogeography, and why they occur in certain localities and not others. It will also be seen that the genetic diversity of these plants belies their ecological uniformity, raising serious doubts for ideas of shared ancestry with their co-inhabitants. Finally, the concept of the mangrove habitat will be enhanced by knowing more about the individuals that provide the structural framework and trophodynamic coherence to this unique ecosystem.

Bunt *et al.*, (1982a) make the point that there are two major problems in identifying mangrove species. The first is deciding what is, and what is not, a mangrove - a problem of better defining the term. The second is a problem of scientific classification, or botanical systematics. Both will be resolved only after this community and the species are better known. This treatment addresses each problem, and presents the recent status of our knowledge, gained principally over the last decade in the Australasian region by the Australian Institute of Marine Science and Graeme Wells with the University of Sydney. The combination of these efforts arguably provide the best continental floristic record for mangroves in the world. Furthermore, these forests are mostly pristine, despite some localized vandalism in more populated areas; notably, in southern Australia where these predominantly tropical habitats are more scarce. This is not to suggest that these are any less valuable though, and recent studies of genetic variation for *Avicennia* in south-eastern Australia depict possible relict Gondwanan ancestors (Duke, 1988). This observation is supported

by the special cold tolerance of these plants, seen in no other mangrove species in the world. Furthermore, the value of these forests is not just of academic interest, it also relates to their cultural and commercial value. The latter is greatly under-rated in Australia, and mangroves in this country have never been threatened by direct commercial exploitation. However, one only needs to look to the north of Australia to see quite a different situation. In Indonesia, Malaysia, Thailand, the Philippines, and just about every under-developed tropical country bordering coastal environments around the world, mangrove forests are under serious threat. This implies a greater urgency on studies of mangrove forests so we can better evaluate this resource, seeking a balance between preservation, restoration and selective utilization.

4.1.1 Mangroves Defined - Plants and Habitat

A mangrove is a tree, shrub, palm or ground fern, generally exceeding one half metre in height, and which normally grows above mean sea level in the intertidal zone of marine coastal environments, or estuarine margins. When referring to the habitat, the term 'mangroves' is used, although perhaps equally often, it is referred to as a 'mangrove forest', and sometimes, a 'tidal forest'. Another term, 'mangal', was proposed for the habitat, but this is considered redundant in view of the previously mentioned, more popular terms. In fact, it is common for individual plants to be referred to, using the term 'mangrove' as an adjective, rather than on its own. Accordingly, an individual tree in the 'mangroves', is commonly referred to as a 'mangrove tree', and so on. Hence, there is only a slight difference to how we refer to other habitats, e.g. rainforests, and the plants found in them.

A greater problem is in the definition itself. Unfortunately, it is not always clear what is a mangrove. Accordingly, species have often been categorized as 'true' mangroves and other taxa, often called 'mangrove associates'. This account makes no attempt to explore this distinction, preferring instead, to focus on those species which best fit the definition. With this in mind, all have been chosen with great care, and they were included only after field evidence of their mangrove affinity appeared undeniable. Most taxa have been commonly viewed in the field by the author, leaving only a few where the detailed descriptions of others have been necessary to gain a better understanding. One example is *Mora oleifera* (= *Mora megistosperma*), which was described from the Pacific coast of Colombia by Von Prah and colleagues (1984, 1990). Another is *Aglaia cucullata* (= *Amoora cucullata*), described in an extensive study of the Bangladesh Sunderbans by Karim (1991). Clearly, there are several additional species which do occur in mangroves from time to time, but the emphasis of the definition is on those which 'normally' grow in the intertidal zone. And, 'normally' was defined on the basis of wide-ranging field observations, where systematic distinctions are known. It will be seen, however, that these distinctions are often unclear, and it is one of the aims of this work to identify such problems, by presenting also the current status of the systematics. This will enable those receptive to the remaining problems, to explore them, and to further improve our understanding of the characteristics and biogeography of each taxon.

4.1.2 Attributes of Mangroves

The combination of morphological and physiological adaptations seen in this diverse and unique group of plants have no equal (Saenger, 1982; Tomlinson, 1986). However, their chief attributes are collectively shared by others in at least three very different habitats, namely deserts, tropical rainforests and freshwater swamps. In xeric habitats, there are many plants, called halophytes, which have both physiological and anatomical adaptations for growing in salty environments. In mangroves, these attributes are necessary to grow in the marine environment, often with their roots immersed in varying concentrations of saltwater. This may change regularly with daily, monthly and annual tidal fluctuations, and with seasonal rainfall and river out-flow. In this way, salinity variations of interstitial waters are often widely and regularly variable. It is believed that this variation at particular sites influences both the types of mangroves that can become established and survive (e.g. Karim, 1991), and their morphology (e.g. Soto and Corrales, 1987; Duke, 1990). Hence, the type and condition of mangroves at particular sites reflect the physical conditions of those sites.

Furthermore, different taxa have different mechanisms for coping with high salt concentrations, and not all have salt-excreting glands on their leaves. Others exclude salt at the roots, although this creates xeric conditions for the plant. Another group also allows low concentrations of salt into their sap, but this is neutralized by its transfer into senescent leaves, or by storing it in their bark or wood. Mangroves also need to cope with growing in water-saturated, often anoxic, substrates. Some of these latter characters are shared with freshwater swamp trees. This lack of gaseous exchange in the substrate requires them to have special breathing structures on the exposed roots and/or trunk. These may be quite different, depending on the taxon. Some, notably *Rhizophora* spp., have aerial prop roots bending down from either the trunk or branches, high above the substratum. Others have shallow, subsurface cable roots with series of vertical, stem-like breathing roots, called pneumatophores. By contrast, in some mangroves, there are no elaborate physical structures, instead numerous small air-breathing lenticels are often present on the trunk. Another essential attribute in this water-saturated environment are structures to support the above ground mass of the tree. This is very important to larger individuals which commonly attain 40 metres in height. So, where roots are unable to penetrate more than a metre or so because of the anoxic conditions, then lateral support structures are essential; i.e., beyond the mutual support provided by the neighbouring community of trees. In these cases, the root structures, already described, contribute a great deal. However, other support structures like trunk buttresses, well-known in tropical rainforests, are also common in mangrove plants.

An important attribute of mangroves is also their viviparous propagules. Again, not all mangroves share this character, and others have lesser degrees of vivipary, while a smaller group have no apparent specialization, compared to their terrestrial counterparts. In most cases, however, the propagules are buoyant for at least a short dispersal phase. The undeniable dispersal specialists, however, are Rhizophoras. These have highly-developed viviparous propagules (in fact, young seedlings), which are believed to be able to endure for several months at sea in a semi-dormant state. In general however, the different propagules, and their various dispersal ranges, reflect the diversity of plant groups found in mangroves.

Table 1. A classification of world plant families with mangrove species (chiefly, Cronquist 1981). Distributions are listed as cosmopolitan (C) or tropical (T), and either widely occurring (pan), or found in specific areas (numbers refer to six global regions in Figure 1). Habit is defined as tree (T), shrub (S), herb (H), climber (C) or ground fern (F). Families underlined have all mangrove species. Orders and families in brackets are those currently less acceptable - note authorities in footnotes.

Sub-class Order	Family	Distrib.	Habit	Name
[Division POLYPODIOPHYTA]				
	Pteridaceae	T,pan	F	Ferns
[Division MAGNOLIOPHYTA - Class Magnoliopsida]				
III. 3.Plumbaginales	Plumbaginaceae ¹	C	S,H	Sea Lavender, Thrift
	(<u>Aegialitiaceae</u>) ¹	T,5,6	S	Club Mangrove
IV. 2.Theales	(Theaceae) ²	T,1,2,5	T,S	Tea, Camellia, Franklinia
	<u>Pellicieraceae</u> ²	T,1,2	T	Panama Mangrove
3.Malvales	Bombacaceae	T,2	T	Baobab, Balsa, Kapok, Durian
	Sterculiaceae ³	T,pan	T,S,H	Bottle Tree, Cocoa, Kola
12.Ebenales	Ebenaceae	T,4	T,S	Ebonies, Persimmon
13.Primulales	Myrsinaceae ⁴	T,4-6	T,S	Tumip-wood, Mutton-wood
	(<u>Aegicerataceae</u>) ⁴	T,5,6	S	River Mangrove
V. 2.Fabales	(<u>Leguminosae</u>) ⁵	T,pan	T,S,H	Peas, Bauhinia, Wattles
	Caesalpiniaceae ⁵	T,pan	T,S	Cassia, Bauhinia, Tamarind
6.Myrtales	Combretaceae	T,pan	T,S,C	Combretum, Quisqualis
	Lythraceae ⁶	T,pan	T,S,H	Crepe Myrtle, Cuphea, Henna
	Myrtaceae	T,6	T,S	Eucalyptus, Bottlebrush, Guava
	Sonneratiaceae	T,4,5,6	T	Mangrove Fig
7.Rhizophorales (Myrt.) ⁷	Rhizophoraceae	T,pan	T,S	Viviparous Mangrove
12.Euphorbiales	Euphorbiaceae	T,pan	T,S,H	Castor-oil, Spurge
16.Sapindales (Rut.) ⁸	Meliaceae ⁹	T,pan	T,S	Mahogany, Rosewood
VI. 3.Lamiales	(Verbenaceae) ¹⁰	T,pan	T,S,H,C	Teak, Verbenas
	<u>Avicenniaceae</u> ¹⁰	T,pan	T,S	Mangrove Olive
6.Scrophulariales	Acanthaceae ¹¹	T,pan	S,H	Black-eyed Susan, Shrimp Plant
	Bignoniaceae ¹²	T,1,2	T,S,C	Tulip Tree, Jacaranda, Catalpa
8.Rubiales (Gentian.) ¹³	Rubiaceae	C	T,S,C	Gardenia, Coffee, Quinine
[Division MAGNOLIOPHYTA - Class Liliopsida]				
II. 1.Arecales	Arecaceae ¹⁴	T,pan	T,S,C	Palms
	(<u>Nypaceae</u>) ¹⁴	T,5,6	S	Mangrove Palm

1. Plumbaginaceae (Heywood 1978, Takhtajan 1980; Cronquist 1981; Tomlinson 1986); Aegialitiaceae (Airy Shaw 1973). Plumbaginaceae in Primulales (Hutchinson 1973); 2. Pellicieraceae (Willis 1966; Takhtajan 1980, Cronquist 1981, Tomlinson 1986). Theaceae (Heywood 1978); 3. Sterculiaceae in Tiliaceae (Hutchinson 1973); 4. Myrsinaceae (Airy Shaw 1973, Heywood 1978; Cronquist 1981, Tomlinson 1986); Aegicerataceae (Hutchinson 1973), Aegiceraceae (de Candolle 1844). Myrsinaceae in Myrsinales (Hutchinson 1973); 5. Caesalpiniaceae (Hutchinson 1973; Takhtajan 1980, Cronquist 1981); Leguminosae (Airy Shaw 1973; Heywood 1978; Morley and Toelken 1983; Tomlinson 1986). Caesalpiniaceae in Leguminales (Hutchinson 1973); 6. Lythraceae in Lythrales (Hutchinson 1973); 7. Rhizophorales (Cronquist 1981, Tomlinson 1986); Myrtales (Hutchinson 1973; Heywood 1978, Takhtajan 1980; Morley and Toelken 1983); Celastrales (Dahlgren 1988; Juncosa and Tomlinson 1988a); 8. Sapindales (Heywood 1978; Cronquist 1981); Rutales (Takhtajan 1980, Muller 1981, Morley and Toelken 1983); 9. Meliaceae in Meliales (Hutchinson 1973); 10. Avicenniaceae (Airy Shaw 1973; Morley and Toelken 1983; Tomlinson 1986); Verbenaceae (Hutchinson 1973; Heywood 1978; Takhtajan 1980; Cronquist 1981). Verbenaceae in Verbenales (Hutchinson 1973), 11. Acanthaceae in Personales (Hutchinson 1973); 12. Bignoniaceae in Bignoniales (Hutchinson 1973), 13. Rubiales (Hutchinson 1973; Heywood 1978; Cronquist 1981, Morley and Toelken 1983); Gentianales (Takhtajan 1980; Muller 1981); 14. Arecaceae (=Palmae) (Hutchinson 1973, Heywood 1978; Takhtajan 1980; Cronquist 1981, Tomlinson 1986). Nypaceae (Airy Shaw 1973).

4.2 Mangrove Floristics and Higher Systematics

The diversity of mangrove plants is best seen in the array of plant orders and families presented in Table 1. There are twenty families, from two plant divisions, including the fern family in the Polypodiophyta, and the remainder in the Magnoliophyta, also known as the angiosperms. Their classification in upper ranks depends on the system used. This account generally follows Cronquist (1981) who described nineteen families with mangrove representatives as part of two classes, six subclasses and 14 orders. However, just two families are exclusively mangrove, and there are no orders or higher ranks with all mangrove taxa. These are underlined in Table 1. Clearly therefore, mangroves are not a genetic entity, but an ecological one. It is interesting to note that even the Rhizophoraceae, often referred to as the 'true mangrove' family, has only four of its sixteen genera inhabiting mangroves. Generally, these families are more commonly represented in tropical rainforests, and most are pantropic in distribution, occurring as trees and shrubs mostly. In addition, the families are better known by their common names and these are usually based on their better-known representatives, including either garden, timber, fruit or medicinal species.

In reference to other systems of classification, there are some notable differences in the status of some mangrove groups (see Table 1). Interestingly, at least three additional, exclusively mangrove families proposed earlier, are now less acceptable. In one case, Aegicerataceae, Cronquist (1981) makes the following statement. "It certainly stands apart from the rest of the Myrsinaceae, but the relationship is not in dispute. *Aegiceras* (the sole representative of the disputed family) is a mangrove, and some of the principal characters by which it differs from typical Myrsinaceae relate to the adaptation of the seed and fruit to the mangrove habit." This clearly presents the view that a plant looks like a mangrove because it grows in a mangrove habitat. It also implies that its genetic divergence from more landward ancestors was less than that required to live in this environment. For the moment, such questions of classification remain arguable, however, at least until future analyses characterize the genetic variation of respective taxa, linking various lineages.

Contrary to the problems of naming higher classification groups, there are few problems in the assignment of generic names. There are twenty-seven genera in total, seventeen are exclusively mangrove (underlined in Table 2), while nine others include non-mangrove species. Notice also that the number of mangrove genera in these families is often relatively low. This feature is also reflected in the number of mangrove species in those genera. Although 50% of genera are monospecific for the mangrove habitat, half of these include greater numbers of non-mangrove species. For the others, the number of mangrove species never exceeds eight, although the addition of putative hybrids adds to the number of taxa by one or two. Regardless, these relatively low numbers are believed to be the result of the harsh conditions imposed within the intertidal habitat. There are expected to be fewer opportunities and less flexibility for natural experimentation and genetic selection. In general, conditions under which mangroves live provide a severe test, requiring a high level of optimized efficiency in each plants utilization of resources. The critical limits on this life-dependant optimization are also believed to be reflected in the structured distribution of species, both locally in zones, and regionally in different climates. This consideration,

Table 2. A classification of all world plant genera with mangrove species (chiefly, Cronquist 1981), including numbers of taxa by family and by genus (numbers in Australia are included in parentheses; for families, Morley and Toelken 1983; for genera, Tomlinson 1986, and personal records). Taxa underlined are those with all representatives in mangrove forests. Numbers of putative hybrids are identified following (+) the number of mangrove species.

Dicot. Sub-class	Order in Mangrove	Name	Family with Mangrove Species		Total Number of Species	Genus with Mangrove Species		
			Total Number of Genera			Name	Non-Mangrove Species	Mangrove Species+ Hybrids'
[Division POLYPODIOPHYTA]								
		Pteridaceae	35		1000	<u>Acrostichum</u>	0	3(1)
[Division MAGNOLIOPHYTA - Class Magnoliopsida]								
III.	3.Plumbaginales	Plumbaginaceae	10(3)		560(9)			
		(<u>Aegialitiaceae</u>)	1(1)		2(1)	<u>Aegialitis</u>	0	2(1)
IV.	2.Theales	(Theaceae)	21-25(1)		550(1)			
		<u>Pellicieraceae</u>	1(0)		1(0)	<u>Pelliciera</u>	0	1(0)
3.Malvales		Bombacaceae	31(3)		225(3)	<u>Camptostemon</u>	0	2(1)
		Sterculiaceae	70(23)		1200(176)	Heritiera	29	3(1)
12.Ebenales		Ebenaceae	3(1)		500(15)	Diospyros	400	1(1)
13.Primulales		Myrsinaceae	35(7)		1000(25)			
		(<u>Aegicerataceae</u>)	1(1)		2(1)	<u>Aegiceras</u>	0	2(1)
V.	2.Fabales	(Leguminosae)	610(172)		18000(1885)			
		Caesalpinjiaceae	150(19)		>2500(85)	Cynometra	70	1(1)

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Table 2 continued

6. Myrtales	Combretaceae	20(3)	500(34)	Mora	19	1(0)
				<u>Conocarpus</u>	0	1(0)
				<u>Laguncularia</u>	0	1(0)
				<u>Lumnitzera</u>	0	2+1(3)
	Lythraceae	25(8)	550(24)	Pemphis	1	1(1)
	Myrtaceae	147(70)	3000(1280)	<u>Osbornia</u>	0	1(1)
	Sonneratiaceae	2(1)	6+(3+)	<u>Sonneratia</u>	0	6+3(5)
7. Rhizophorales	Rhizophoraceae	16(5)	120(13)	<u>Bruguiera</u>	0	6(5)
(Myrt.)				<u>Ceriops</u>	0	3(3)
				<u>Kandelia</u>	0	1(0)
				<u>Rhizophora</u>	0	6+3(4)
12. Euphorbiales	Euphorbiaceae	300(53)	7000(215)	Excoecaria	35-40	2(1)
16. Sapindales	Meliaceae	50(11)	600(34)	Aglaia	100	1(0)
(Rut.)				Xylocarpus	1	2(2)
VI.3. Lamiales	(Verbenaceae)	75(17)	3000(62)			
	<u>Avicenniaceae</u>	1(1)	8(2)	<u>Avicennia</u>	0	8(2)
6. Scrophulariales	Acanthaceae	250(21)	2500(40)	Acanthus	30	2(2)
	Bignoniaceae	120(5)	800(9)	Dolichandrone	9	1(1)
8. Rubiales	Rubiaceae	500(42)	7000(203)	<u>Scyphiphora</u>	0	1(1)
(Gentian.)						
[Division MAGNOLIOPHYTA - Class Liliopsida]						
II. 1. Arecales	Areaceae(Palmae)	210(21)	2800(52)			
	(Nypaceae)	1(1)	1(1)	<u>Nypa</u>	0	1(1)

therefore, would be expected to play a large part in the biogeography and evolution of particular mangrove habitats.

Mangrove forests are dominated by two orders, the Myrtales and Rhizophorales (Table 2), often combined by some authors as a larger Myrtales order (Morley and Toelken, 1983). These comprise 25% of all mangrove families and 50% of all species. They also demonstrate a high degree of specialization for the habitat, since all but one of the ten genera are exclusively mangrove. The remaining one, *Pemphis*, has only one other species, located inland as an isolated population on the island of Madagascar. In addition, the Rhizophoraceae is recognized as a highly adapted and apparently well-advanced family, although it bears some putatively primitive characters (Juncosa and Tomlinson, 1988b). These characters are somewhat subjective, however, and while Sporne (1969) ranked it with less-advanced angiosperms, this view was not endorsed by recent more detailed appraisal (Dahlgren, 1988; Juncosa and Tomlinson, 1988b). Evidence of fossil pollen is more precise, and the earliest records of Myrtales (including the Rhizophoraceae) date from the upper Cretaceous, approximately 20 million years after the first records of angiosperms (Muller, 1981). The latter suggests that mangrove habitats were occupied very early after the evolution of angiosperms, and at least these ten families have had relatively long histories of development. Orders are also characterized by the inclusion of all putative hybrids found in mangrove forests today. These are from three genera, *Lumnitzera*, *Sonneratia* and *Rhizophora*. Furthermore, in each of them, the ratio of species to putative hybrids is 2:1. For the two genera with six species, this suggests that only one species crosses with some of the others. This may be the result of one widely distributed species occurring sympatrically with its otherwise allopatric conspecifics. In total, there are 69 mangrove species including putative hybrids, and 39 of them, comprising representatives of all polyspecific genera, are found in Australia. This clearly indicates the key position of Australia in the phylogeography and evolution of mangroves.

4.3 Global Distribution Patterns and Species Systematics

Mangroves are distributed according to three important scales, namely their coastal range, their location within an estuary, and their position along the intertidal profile. Each of these will be discussed, along with a brief review of the problems in naming species.

On a global scale, mangrove plants are found throughout tropical regions of the world (Figure 1). More precisely, there is a conspicuous tropical distribution pattern with major deviations matching the presence of warm and cold oceanic currents. Latitudinal ranges therefore tend to be broader on eastern continental margins and more constrained on their western sides; for example, in the North and South Atlantic Oceans, the colder Canaries and Benguela Currents, each moving toward the equator from the north and south respectively, reduce the lineal extent of warmer coastline for west Africa. Conversely, on the east coasts of North and South America, the warmer poleward moving Florida and Brazil Currents extend the warmer coastline. Mangroves generally match the winter 20°C isotherm in respective hemispheres, suggesting the profound importance of water temperature to this

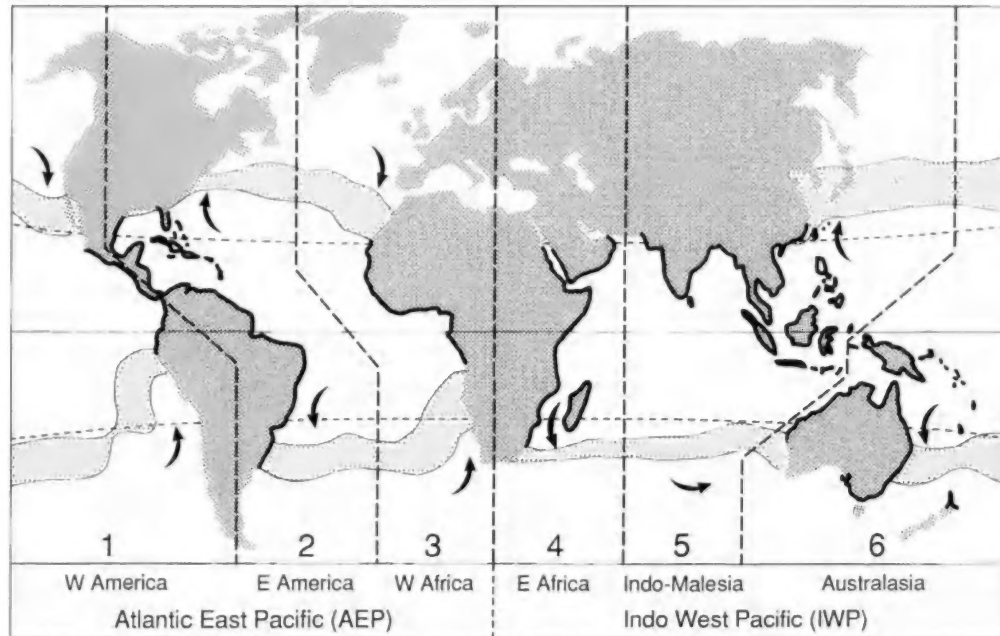


Figure 1. World distribution of mangroves showing their coastal extent (outlined), range of 20°C isotherms in January and July, major ocean currents influencing latitudinal range around the tropic lines, and six biogeographic regions grouped in two global hemispheres discussed in the text. Notice that the poleward extent of mangroves is usually associated with the winter position of the 20°C isotherm, except for, the east coast of South America (region 2), Australia, and the North Island of New Zealand (all in region 6).

habitat. There are three important exceptions to this pattern, however, and all occur in the southern hemisphere, notably along the coastlines of eastern South America, around Australia, and across the North Island of New Zealand. This could be the result of specific, small-scale extensions of warmer currents, but it appears more likely that these populations are relict, representing refuges of more poleward distributions in the past.

These exceptions notwithstanding, mangroves are found chiefly in tropical latitudes where their global dispersal by specialized water-buoyant propagules is apparently constrained by both wide bodies of water and land masses blocking the equatorial flow of tropical waters. Today, there are four major barriers, influencing the dispersal of most warm coastal marine organisms (Briggs, 1974), including the continental land masses of Africa and Euro-Asia, North and South American continents, North and South Atlantic Oceans, and the eastern Pacific Ocean. The relative effectiveness of each of these barriers differ, however, depending on geological history, and the dispersal-establishment ability and evolution of each taxon. There are two barriers which appear to have been reasonably effective during recent geological time, namely the African Euro-Asian continents, and the Pacific Ocean. Thus, mangrove species, and indeed most tropical, shallow-marine coastal habitats, are divided into two global hemispheres (Figure 1), the Atlantic East Pacific (AEP), often referred to as the New World, and the Indo West Pacific (IWP), or Old World. These more-

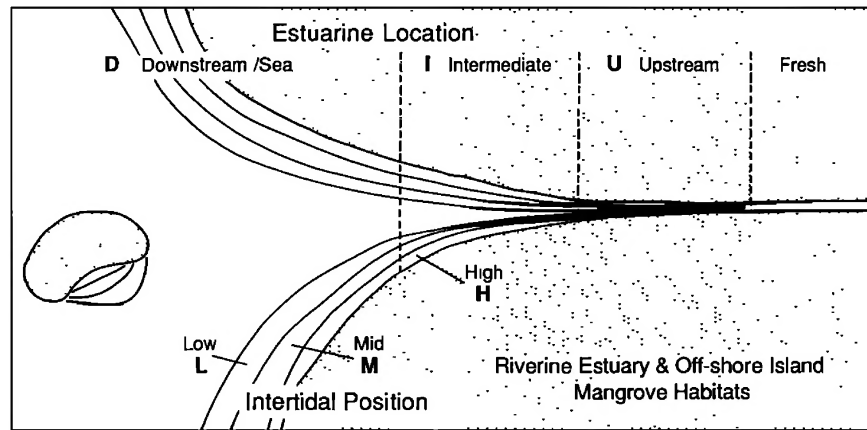


Figure 2. A sketch map delineating the two common mangrove habitats described and discussed in the text, and used in Table 3. Each is divided into three categories: estuarine location with, downstream, intermediate and upstream; and, intertidal position with, low, mid and high.

referred to as the New World, and the Indo West Pacific (IWP), or Old World. These more-or-less equal portions of the earth also have equivalent areal extents of mangrove forests (Saenger *et al.*, 1983), and represent centres of secondary radiation because they share three major mangrove genera. The AEP has fewer species, however, and fewer additional genera, although it spans two extant barriers. Meanwhile, the most diverse flora is seen in the IWP, constrained between two existing barriers. Based on species presence, this may also be divided into three regions, making a total of six for the world (Figure 1), including (1) western Americas, (2) eastern Americas, (3) western Africa, (4) eastern Africa, (5) Indo-Malesia, and (6) Australasia (Figure 1).

Mangroves are distributed according to at least two other scales, namely their location within an estuary, and their position along the intertidal profile. The latter has often been referred to as zonation. Nevertheless, both may be conveniently summarized in six categories (Figure 2), based on the two specific factors, estuarine location, and intertidal position. Each can be divided into three, including: downstream, intermediate and upstream estuarine, and, low, mid and high intertidal. Downstream also includes off-shore island communities, similarly divided into the three intertidal categories. These are essentially a simplification of the five intertidal inundation classes described by Watson (1928). Hence, 'low intertidal' represents areas inundated by medium high tides and flooded >45 times a month (Watson classes 1 & 2), 'mid intertidal' represents areas inundated by normal high tides and flooded from 20 to 45 times a month (Watson class 3), and 'high intertidal' represents areas inundated <20 times a month (Watson classes 4 & 5). By contrast, estuarine location categories are less well-defined, since the specific physical parameters are not fully understood or quantified for many tropical riverine estuaries. Hence, in this treatment, the proportional distance from the mouth of the estuary is used, where downstream represents the lower third of the estuary including off-shore islands, intermediate represents the middle third of the estuary, and upstream represents the upper third. Knowing the variability in

estuarine systems, reflected mainly in intermediate locations, these categories do not adequately describe them, but for the time being, downstream and upstream divisions are useful in identifying those river systems characterized by the presence of particular mangroves. Hence, for example, a species might be known as a low intertidal, upstream specialist.

All mangrove species and putative hybrids in the world are listed in Table 3. Understandably, this compilation identifies several problems. As discussed earlier, it is one thing to have difficulty with the definition of a mangrove and deciding whether a particular species should be included in this list, but quite another, to be unable to confidently assign a name to each taxon. This is not only a problem with rare taxa, rather it applies more often to common plants. For instance, the systematic distinction between *R. mucronata* in eastern Africa and *R. stylosa* in Australia remains unclear (Duke and Bunt, 1979; Tomlinson, 1986). This becomes further confusing in places where they apparently overlap, like Malesia. And in Australia, the species referred to *R. mucronata*, is not like that in eastern Africa. This problem with *Rhizophoras* extends further when considering their putative hybrids. In Australia, the hybrid between *R. stylosa* and *R. apiculata* is known as *R. X lamarckii*, and its occurrence matches the overlap of its putative parents. In south-eastern India, there is a taxon that fits the description of *R. X lamarckii* (personal observation). If it is a hybrid, and the parents are *R. mucronata* and *R. apiculata*, as listed for the region, then it cannot be *R. X lamarckii*. That is, unless *R. X lamarckii* is not a hybrid, but this would conflict with recent evidence (also note Duke *et al.*, 1984). It is more likely that *R. mucronata* in India and eastern Africa is the same species as *R. stylosa* in Australasia, and that the range of *R. X lamarckii* is far greater than presently listed. Of course, this also means that the true name of the *R. mucronata* - *R. stylosa* parent must be cleared up. Then the name of the plant in Australasia, called *R. mucronata*, can also be settled. Clearly, there is an urgent need to resolve this situation before any realistic assessment of the biogeography and evolution of *Rhizophoras* can be confidently discussed. Furthermore, this problem with *Rhizophoras* is not restricted to the IWP, because those in the AEP have a comparable question of hybrid status for *R. X harrisonii*, with putative parents, *R. mangle* and *R. racemosa*. Other, mostly polyspecific genera, have equivalent systematic problems, and the size of these problems appear to be a function of each groups diversity. Furthermore, because specific identities are generally better-known in most countries, the main gap now appears to be more detailed comparisons between regions. This would resolve problems described for *Rhizophora*, and other taxa, including, *Sonneratia lanceolata*, *Avicennia marina* varieties, and so on (Table 3). However, this is certainly not to suggest that further intra-regional studies are not necessary. Some examples of these include, the distributions of *Acanthus ebracteatus* and species of the genus *Acrostichum*, as well as investigations of the presence of *Sonneratia* X 'merauke' in northern Australia and southern New Guinea.

The ranges of each taxa, based on their presence or absence in the six biogeographic regions, are listed also in Table 3. The greatest species diversity is found in the IWP with 58 taxa, almost six times more than the AEP with 12. There are 69 altogether, so there is only one species common between hemispheres, namely *Acrostichum aureum*, a mangrove fern. It is possible that *Rhizophora samoensis* is the same as *R. mangle* (Tomlinson, 1986), but this also requires more attention. Generic diversity is more conservative, however, with 7 genera

in the AEP, 23 in the IWP, and three in common throughout the six regions. Furthermore, with respect to families, the AEP is virtually a subset of those in the IWP, with the exception of Pellicieraceae. The region with least species is western Africa (region 3) in the AEP with seven taxa, whilst Indo-Malesia (region 5) in the IWP has more than 49. In the IWP, the east African region is most depauperate with only ten taxa, notably equivalent to regions in the AEP. Their respective species compositions, however, are completely different.

The genera and families shared by the IWP and AEP, and the minimal overlap of species, provides evidence of an earlier long period of continuity or connection between regions that has been interrupted also for a long period. Furthermore, present day distributions of species do not conform with expectations either, based on their respective dispersal-establishment abilities and existing barriers. For example, note the common presence of several AEP taxa in all three regions, while others are restricted. This is shown best in the three AEP *Avicennia* which share habitat preferences and propagule characteristics, but have completely different ranges. Also note the presence of *Rhizophora samoensis* in Australasia. Clearly, such disjunctions provide clues of past distributional ranges, and hypotheses on the evolution of mangroves need to explain the presence of each species.

There is a general trend between genera and distributions, listed in Table 3, such that genera with the greatest number of species (plus putative hybrids; taxa/genera), consistently occur in the greater number of biogeographic regions ($r = 0.689$, $n = 26$, $P < 0.001$). Conversely, those with fewer species occur in fewer regions, notably seen for genera with one or two species which only occur in one or two regions (Figure 3). These make up > 50% of mangrove genera. All larger polymorphic genera (3-9 taxa/genera) are found in three or more regions, i.e. excluding the non-angiosperm family with the pantropic fern, *Acrostichum aureum*, apparently found in all regions. Nevertheless, this trend confirms the idea that more widely distributed taxa have greatest genetic diversity. Geographic isolation therefore appears to be the major mechanism promoting diversity and speciation in mangrove plants.

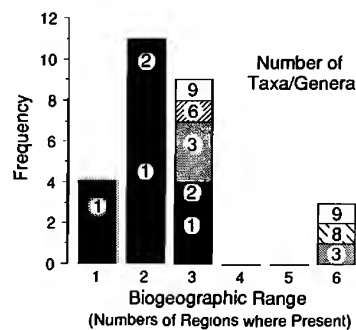


Figure 3. A frequency plot comparing biogeographic range (defined as number of regions, from Figure 1) with the number of taxa per genera for all mangrove genera in the world (Tables 2 & 3). Note that genera with one or two species are restricted mostly to two regions, while those with more than two genera always range over three or more regions.

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Table 3. A classification of all mangrove species in the world (chiefly, Cronquist 1981), including their global distribution (see Figure 1), and common habitat (see Figure 2). Distribution is scored for six biogeographic regions as, present o, widely distributed @, or doubtful ?. Upstream riverine or estuarine location listed as downstream (D), intermediate (I) and upstream (U). Topographic or intertidal position listed as low (L), mid (M) and high (H). These records are based chiefly on Ding Hou (1960), Percival and Womersley (1975), Duke *et al.*, (1981), Von Prah (1984), Tomlinson (1986), Duke and Jackes (1987), Von Prah *et al.*, (1990), Duke (1991a), Duke (1991b), and Karim (1991). Number superscripts refer to systematic problems, outlined in the footnotes.

Diet. Sub-class	Order in Mangrove	Family in Mangrove	Genus in Mangrove	Species in Mangrove	Global Biogeographic Regions						Common Habitat	
					1	2	3	4	5	6	Estuary Location	Intertidal Position
[Division POLYPODIOPHYTA]												
III.	Plumbaginales	Pteridaceae	Acrostichum ¹	danaeifolium	⊗	⊗					I	H
				aureum	○	○	○	○	○	I	H	
				speciosum				⊗	⊗	I	H	
[Division MAGNOLIOPHYTA - Class Magnoliopsida]												
IV.	Theales Malvales	Plumbaginaceae	Aegialitis	roundifolia					⊗		?	?
				annulata					○	⊗	D	M,H
		Pellicieraceae	Pelliciera	rhizophorae	⊗	○					I,U	M,H
				Camptostemon				⊗		?		H
				philippensis								
		Sterculiaceae	Heritiera	schultzei					⊗		D,I	L,M
				littoralis				⊗	⊗	I	H	
				fomes				○		U	H	
		Ebenaceae	Diospyros ²	globosa					○		U	H
				ferrea								H
V.	Fabales	Myrsinaceae	Aegiceras	comiculatum					⊗	⊗	I,U	M,H
				floridum					⊗		I,U	L
										?	?	?
		Caesalpiniaceae	Cynometra	iripa					⊗	⊗	I,U	H
				Mora				⊗		U	H	
				oleifera				⊗	⊗	D	H	
	Myrtales	Combretaceae	Conocarpus	erectus								H

Table 3 continued

Rhizophorales	Rhizophoraceae	Laguncularia racemosa	©	©	©	D,I	M,H
		Lumnitzera racemosa	©	©	©	D	M,H
Lythraceae Myrtaceae Sonneratiaceae		X rosea			?	I	H
		littorea			©	I	M
		Pemphis acidula			©	D	H
		Osbornia octodonta			©	D	M,H
		Sonneratia apetala			©	U	L,M
		griffithii			©	D	L
		alba	©		©	D	L
		X sp. ³			©	?	?
		ovata			©	D	H
		X guineai			©	I	L,M
		caseolaris			©	U	L
		X 'merauke' ⁴			?	I	M
		lanceolata ⁵			©	U	L
		Bruguiera gymnorrhiza	©		©	D,I	M,H
Rhizophorales	Rhizophoraceae	sexangula			©	I,U	M,H
		exaristata			©	I,U	H
		hainesii			©	I	H
		parviflora			©	D,I	M
		cylindrica			©	D,I	M
		Ceriops tagal	©		©	D,I	M,H
		decandra			©	I	M,H
		australis ⁶			©	D,I	H
		Kandelia candel			©	D	L
		Rhizophora racemosa	©	©	©	D,I	M
		X harrisonii	©	©	©	D, ⁷	L, ⁷
		mangle			©	D,I	L,M
		samoensis ⁷			©	D,I	L,M
		X selala			©	?	?
Rhizophorales	Rhizophoraceae	stylosa			©	D,L	L,M
		X lamarckii			©	D,I	M
		apiculata ⁸			©	I	M

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Euphorbiales	Euphorbiaceae	Excoecaria mucronata ⁹	⊙	⊙	⊙	⊙	I,U	L,M
		Excoecaria agallocha ¹⁰	?	⊙	⊙	⊙	D,I,U	M,H
		indica		⊙			D,I	L,M
		Aglaia cucullata ¹¹		⊙			U	M
Sapindales	Meliaceae	Xylocarpus granatum	⊙	⊙	⊙	⊙	I	M,H
		mekongensis		⊙			I	M,H
		Avicennia germinans ¹²	⊙	⊙	⊙		D,I	M,H
		bicolor	⊙				D	H
VI. Lamiales	Avicenniaceae	schaueriana		⊙			D	M,H
		marina ¹³	+		⊙	⊙	D,I	L,M,H
		alba			⊙	⊙	D	L,M
		rumphiana ¹⁴			⊙	⊙	D	H
		officinalis			⊙	⊙	I	L
		integra				⊙	I	L
		Acanthus ebracteatus ¹⁵			⊙	⊙	I	M,H
		ilicifolius			⊙	⊙	I,U	M,H
		Dolichandrone spathacea			⊙	⊙	U	M
		Scyphiphora hydrophyllacea			⊙	⊙	I	H
Scrophulariales	Acanthaceae							
Rubiales	Bignoniaceae							
VIII. Arecales	Arecaceae	- Class Liliopsida ¹⁶						
		Nypa fruticans ¹⁶	+	+	⊙	⊙	U	L,M,H

1. *Acrostichum* species are poorly identified in most records (Tomlinson, 1986); 2. *Diospyros* reported by Duke *et al.* (1981) is not adequately described and the species name is provisional; 3. *Sonneratia* X sp. = putative hybrid *S. alba* X *S. ovata* (Muller and Hou Liu, 1966); 4. *Sonneratia* X 'merauke' represents the putative hybrid, *S. alba* X *S. lanceolata* (Duke and Jackes, 1987); 5. *Sonneratia lanceolata* and *S. caseolaris* in Australasia lack clear distinction in descriptions from Indonesia and SE Asia (Duke and Jackes, 1987); 6. *Ceriops australis* and *C. tagal* were shown in electrophoretic studies to be sibling species (Ballment *et al.*, 1988); 7. *Rhizophora samoensis* lacks clear morphological distinction from *R. mangle* (Tomlinson, 1978); 8. *Rhizophora apiculata* has cork warts (i.e., underleaf spots) on leaf specimens from Indo-Malesia, while these are not present in southern New Guinea and northern Australia (Duke and Bunt, 1979); 9. *Rhizophora mucronata* from E Africa and SE Asia is not clearly distinct from *R. stylosa* (compare Ding Hou, 1960, Tomlinson, 1986 and Duke and Bunt, 1979). Furthermore, *R. mucronata* in Australasia is possibly a different species (Duke and Bunt, 1979); 10. *Excoecaria agallocha* is not reliably known to occur in E Africa (Tomlinson, 1986); 11. *Aglaia cucullata* (= *Amoora cucullata*) habitat described by Karim (1991); 12. *Avicennia germinans* (= *A. africana*) was reportedly introduced to W Africa (Gunn and Dennis, 1976), although this claim cannot be substantiated (Tomlinson, 1986); 13. *Avicennia marina* var. *australasica* was introduced (+) to Mission Bay, California (pers. comm.); 14. *Avicennia rumphiana* (= *A. lanata*) habitat and distribution described by Duke (1991a); 15. *Acanthus ebracteatus* is not clearly identified from *A. ilicifolius* in most accounts (Tomlinson, 1986); 16. *Nypa fruticans* was apparently introduced (+) into W Africa and E Central America (Duke, 1991b).

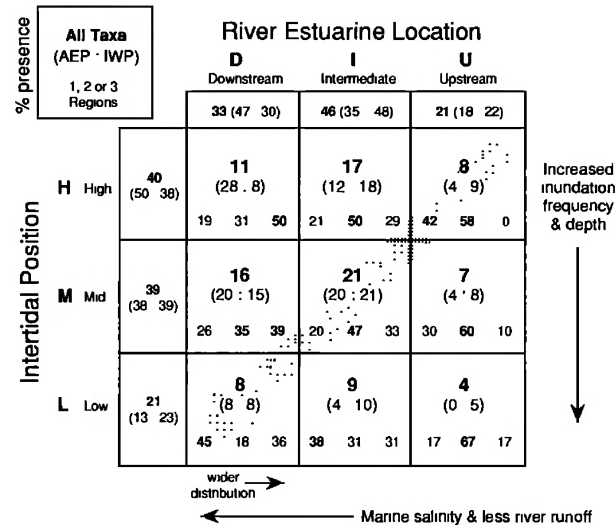


Figure 4. A two-way tabulation showing the % presence in the two common habitat categories, estuarine location and intertidal position (Figure 2), of all mangrove taxa in the world (Table 3). The categories are further divided by, presences in both the Atlantic East Pacific (AEP) and the Indo West Pacific (IWP), and for the presence in one, two or three biogeographic regions (Figure 1). This figure shows the taxa are found throughout most paired combinations of habitat types. The diagonal arrow is indicative of greater 'mangrove-ness' of taxa, notably by being more specialized for life in the intertidal environment characterized by increased inundation and higher salt concentrations.

There is also isolation at other scales of distribution, notably in the specialization of particular mangroves for certain habitats. These data, listed in Table 3, are summarized in Figure 4. It displays percent frequencies of recorded presences in the various habitats and for their paired combinations. The presence of mangrove species in the two habitat types was shown to be quite uniform, with an expected maximum frequency of 21% in mid-intertidal, intermediate combinations, and a minimum of 4% in the low-intertidal, upstream. By excluding mid-intertidal and intermediate sites, there is an apparent trend toward higher frequencies (11%) in high-intertidal downstream sites. On closer inspection, however, this was due almost entirely to species in the AEP with a maximum frequency of 28% in this habitat combination. They also have no presence in the low-intertidal, upstream. It is suggested that this difference between regions might reflect different levels of evolutionary progress of the mangrove environment. For example, it is likely that the evolution of mangroves might have progressed via the high-intertidal upstream to the low-intertidal downstream, based on their progress in adapting to both increased salinity and inundation frequency. Of course, they may also have adapted in a less balanced way, possibly by attaining halophytic attributes first, and adapting to lower intertidal positions second. If this was the case, then the taxa in the AEP could have retained ancestral characteristics, reflecting a tendency for earlier halophytic progenitors. By contrast, IWP taxa demonstrate a more mixed association with the various habitat combinations, suggesting either a more advanced stage of development for these mangrove forests, or a balanced compliment of progenitors from both upstream and downstream locations.